BONADUCECYTHERIDAE, A NEW FAMILY OF CYTHERACEAN OSTRACODA, AND ITS PHYLOGENETIC SIGNIFICANCE

K. G. McKenzie

In general, life consistently (stubbornly, perhaps) refuses to recognize the neat compartments formulated for it by the intuitions of taxonomists whether their interests be heirarchic or phylogenetic. Only rarely do the classifications of even a decade ago satisfy the needs of researchers aware of recent advances in knowledge. In all major groups, an honest assessment of the situation recognizes the occurrence of taxa which are unclassifiable under the present systems. Ostracoda conform to this generalization, and ostracode taxonomists are emphatic in stating the urgency of the need for a revision of the current classifications as presented by the Russian and American Treatises (Orlov, 1960; Moore, 1961). The first moves towards a new classification for Ostracoda were taken at the fifth Ostracoda Congress at Hamburg (August, 1974) with the circulation of a paper by Hartmann & Puri (1974), but the general ferment was already implicit in recent papers by a number of other authors (Grundel, 1967; Poulsen, 1969; Danielopol, 1972; Kozur, 1972; McKenzie, 1972; Kornicker, 1974; Kornicker & Sohn, in press). A further discussion was arranged for the sixth congress at Vienna in 1976.

The Ostracode group which probably presents the greatest problem for researchers attempting to achieve a classification which satisfies both neontologists and palaeontologists, is the Podocopa. This is the largest group of living Ostracoda and it is also abundantly represented in the fossil record from the Ordovician onwards. The new family described below belongs in the Podocopa, and its description necessitates yet another look at the classification of that group.

> Phylum CRUSTACEA Linnaeus Subphylum OSTRACODA Latreille 1802 Class Podocopa Müller 1894 Order PODOCOPIDA Sylvester-Bradley 1961 Suborder PODOCOPINA Swain 1961 Superfamily CYTHERACEA Baird 1850 Family BONADUCECYTHERIDAE, new family

Diagnosis.—A family of small cytheracean ostracodes characterized by the fact that in males expanded seminal vesicles are housed within the duplicature, and by the development of the unguis of the male's first limb (PI) into a clasping structure. Except for the male PI, endopods of the thoracic limbs have 4 segments. The carapace is extremely flattened ventrally and tapers anteriorly where it is broadly rounded. Posteriorly, it is acuminate with a distinct selvage in both valves. Anteroventrally, the valves have a pronounced gape. The line of concrescence is expressed at both the inner and outward ventral margins and is invaginated anteriorly and posteriorly. The central muscle scar group comprises 3 adductors in an oblique row and a single frontal scar. The hinge is adont. The favored environment for the taxon is interstitial.

Bonaducecythere, new genus

Name.—For Dr. G. Bonaduce, of Stazione Zoologica, Napoli, who collected the material.

Type-species.—Bonaducecythere hartmanni n. sp.

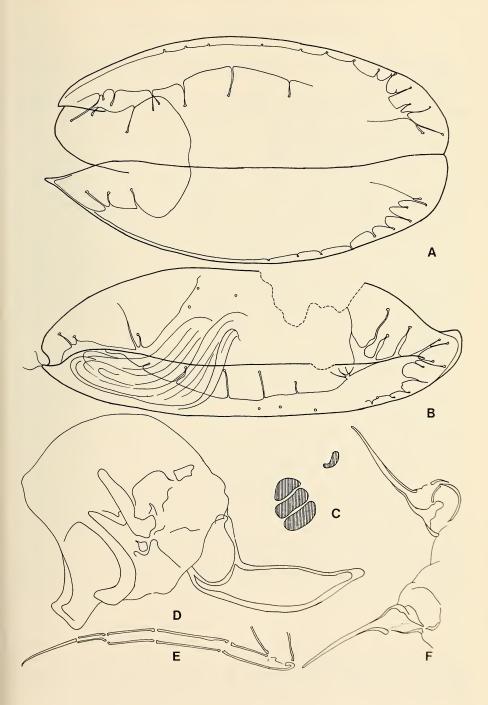
Diagnosis.—A genus of bonaducecytherid cytheraceans characterized by small size and the other features listed in the family diagnosis.

Discussion.-The line of concrescence in this genus may be compared with those of the genera Microxestoleberis Müller, 1894, and Aspidoconcha de Vos, 1953, which are similarly expressed at both the inner and outward ventral margins. These genera, however, possess the typical arcuate evespot and seive-type normal pore canals of xestoleberidids, characters which do not occur in the new genus. They are broader dorsally with respect to their length than is Bonaducecythere. Other genera from an interstitial habitat have been listed by Hartmann (1973) but none of them is close to Bonaducecythere either in carapace morphology or in soft anatomy. Since Aspidoconcha is a symbiont, it is worth pointing out that there are likewise few similarities between the new genus and the symbiont genera listed in McKenzie (1972b). The cytheracean families involved in these several comparisons include: Paradoxostomatidae (characterized by specialized mouthparts); Xestoleberididae (considered above); Microcytheridae (different muscle scars and hinge elements); Psammocytheridae (both ends rounded); Kliellidae (fused zone narrow or absent); Parvocytheridae (one pair less of thoracic limbs, different muscle scar pattern); Loxoconchidae (sieve-type normal pore canals, different hinge elements); Cytheridae (sieve-type normal pore canals, few, straight radial pore canals); Krithidae (different line of concrescence as exemplified by Microloxoconcha Hartmann 1954)-all as diagnosed by Hartmann and Puri (1974).

 \rightarrow

264

Fig. 1. Bonaducecythere hartmanni A, Female carapace in dorsal view, anterior to the right, $\times 625$; B, Male left valve in lateral view, anterior to the right, $\times 625$; C, Adductors scars and frontal scar, male left valve; D, Male hemipenis; E, Female PI; F, Female posterior body.



Bonaducecythere hartmanni, new species Figs. 1–2

Name.—For Prof. Dr. G. Hartmann, University of Hamburg, who dissected the female.

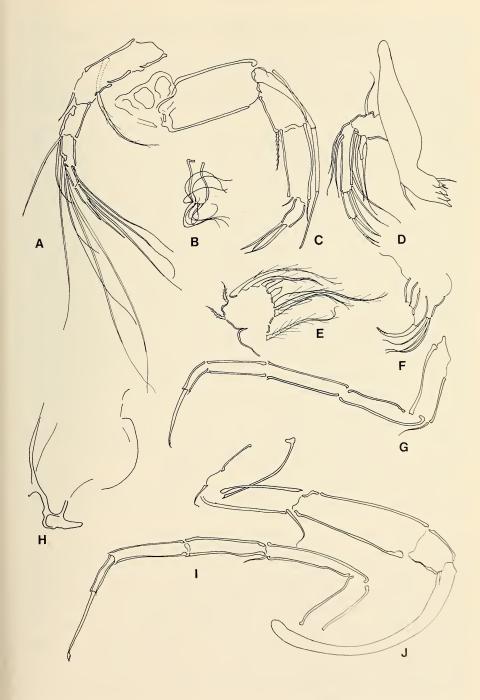
Description.—Carapace small, thin-shelled, smooth, elongate, the height little more than 1/3 the length, breadth less than half the length, right valve overlapping the left valve dorsally and ventrally, anterior broadly rounded with a flattened anterodorsal lip, posterior acuminate with 2 short posteroventral setae in each valve, dorsum convex, venter broad and markedly flattened. In ventral view, the carapace is seen to gape anteriorly. Internally, the most striking feature is the very prominent selvage and the distinctive line of concrescence which is deeply invaginated anteriorly and posteriorly. Radial pore canals are sometimes branched anteriorly and posteriorly, elsewhere simple and straight or curved; those at the outer ventral margin very short; normal pore canals scattered, except anteriorly where they are bunched and numerous, simple, open. Hingement adont, with accommodation for the right valve by the left. Muscle scar pattern consisting of an oblique series of 3 adductors plus a single frontal scar and (?) 2 small mandibular scars. Sexual dimorphism of the valves is not marked (Figs. 1A-C).

Antennule 6-segmented; length ratios of the segments being 38:17:20:19: 13:12; first segment with a long hirsute dorsomedial bristle; second segment with a shorter dorsodistal bristle; third segment with 2 dorsodistal bristles; fourth segment with 4 dorsomedial bristles and 6 dorsodistal bristles; fifth segment apparently bare; sixth segment with 2 terminal bristles (Fig. 2A). Antenna with a 3-segmented endopod; length ratios of the segments being 32:45:18; first segment with 2 short ventrodistal and 2 short dorsodistal bristles; third segment with 2 powerful terminal ungues and a weaker unguis plus a short ventrodistal bristle; exopod 3-segmented with a sensitized tip (Fig. 2C). Mandible coxale with 6 teeth decreasing in strength from front to rear, the anterior teeth with intervening "toothbrush" bristles; epipod with 1 or 2 Strahlen; endopod 3-segmented; length ratios of the segments being 20:40:17; first segment with a clump of 4 ventrodistal bristles, at least 2 of these armed with numerous spiky hairs; second segment with 2 proximodorsal pilose bristles and 2 ventrodistal bristles; third segment with 2 terminal ungues and a terminal bristle

 $[\]rightarrow$

Fig. 2. Bonaducecythere hartmani, male. For complete chaetotaxy of limbs illustrated in this figure refer to the text. A, Antennule; B, Brush-shaped organ; C, antenna; D, Mandible; E, Maxilla epipod; F, Maxilla palp and lobes; G, PII; H, Lower lip; I, PIII; J, PI.

VOLUME 90, NUMBER 2



(Fig. 2D). Maxilla comprising a 2-segmented palp and 3 lobes; the first segment of the palp carrying 4 distal bristles; the second segment with 4 terminal bristles, 2 of these unguis-like; of the lobes, the first lobe may only have 2 terminal bristles but the second and third lobes each appear to have at least 4 terminal bristles; epipod with 2 shorter Strahlen and about 10 other Strahlen (Fig. 2E, F). First thoracic limb (PI) dimorphic between male and female.

Male limb comprising a protopod with a ventromedial and ventrodistal bristle; endopod 3-segmented; first segment with a ventrodistal bristle; second segment bare; third segment with a very short ventrodistal bristle and a long curved sclerotized clasping unguis rounded at the tip (Fig. 2]). Female limb (PI) with a 4-segmented endopod and a "normal" slender terminal unguis (Fig. 1E). PII and PIII non-dimorphic between males and females, each with a 4-segmented endopod and a slender terminal unguis (Figs. 2G, I). Male brush-shaped organs with 12 or more setae (Fig. 2B). Posterior of the body dimorphic, consisting in the female of paired caudal (?) processes which do not occur in the male (Fig. 1F). Genitalia of female could not be observed. Male with paired hemipenes, each characterized by a very prominent anterior processus otherwise not observed in detail (Fig. 1D). Seminal vesicles occurring as several loops apparently coiled within the posterior duplicature, a feature unique among cytheraceans. The species is blind in both sexes. Mouthparts as far as could be observed appear to be unspecialized with the mandible endopod and maxillar lobes operating as food forwarding and/or gathering structures. Evidently, the anteroventral gape of the valves is a modification which facilitates ventral feeding.

Dimensions.-Male: Length 0.21 mm, height 0.07 mm, breadth 0.09 mm; Female: Length 0.20 mm, height 0.06 mm, breadth 0.09 mm.

Material.-Two adult males and 5 adult females.

Locality.—St. Pauls Bay, Malta; on the south side of the Bay in front of the lido at St. Paul-il-Banar, at about 10 m out from the shore; depth 4 to 5 m; coarse and medium sized sand; the collection was made from between the bases of living *Posidonia*; 9 April 1974.

Discussion.—In a review of interstitial ostracodes, Hartmann (1973) pointed out several adaptations which appear to be common to many taxa. These include blindness, reduction in the number of limbs and segments, reduction in reproductive parts, a distinctive shape, and alteration of some limb structures. Bonaducecythere hartmanni illustrates several of these features, in particular those related to blindness and carapace shape. The flattened carapace with a tapered anterior is well adapted to interstitial life among Posidonia. The prominent anteroventral gape of the valves is apparently unique to this taxon and seems to favor ventral feeding. The animal is evidently a detrital feeder since the mandible and mouth-

parts are not specialized, as in Paradoxostomatidae, for symbiotic feeding on *Posidonia* and other marine plants.

Phylogenetic Significance

Before discussing the phylogenetic significance of Bonaducecythere, it is necessary to enlarge a little upon the concept of the Phylum Crustacea, since this category is a relatively new one for students of arthropods. After a lifetime of research, Manton concludes that ". . . the Arthropoda are probably polyphyletic and that arthropodisation has occurred at least three times, forming the phyla Crustacea, Chelicerata and Uniramia (Onychophora, Myriapoda, Hexapoda)" (Manton, 1973, p. 111). Her con-clusions have been substantiated by the results of 'fate map' embryological research (Anderson, 1973). Manton stresses that convergences of structure are numerous between arthropodans of different taxanomic positions, and the author has also made this point (McKenzie, 1970). Once the concept of Crustacea as a phylum rather than as a class is considered in terms of the fossil record some previous problems disappear. Thus, no Uniramia are known with certainty before the Silurian (the marine Cambrian Burgess Shale taxon, Aysheia Walcott 1912, is an homeomorph of modern terrestrial Onychopora, not an ancestor, since it apparently lacks arth-ropodan cephalic structures and had strikingly different habits of life; e.g. it respired differently and must have fed differently). Considerations pertaining to the evolution of the predominantly terrestrial uniramians, therefore, need not cloud the perceptions of workers interested in the older predominantly aquatic crustaceans. And, since the taxonomic position of the trilobites remains anomalous, it is scarcely special pleading to suggest that more attention be paid by crustacean phylogeneticists to the Ostracoda which have the longest continuous and probably the most abundant record in the phylum. This comment is reinforced by the fact that some early fossils previously assigned to the crustacean group Phyllocarida or to riberioids have now been shown to have molluscan affinities (Runnegar and Pojeta, 1974).

The distinctiveness of the Ostracoda has never been questioned and their combination into a taxon at the subphylum level follows logically from the recognition of the Crustacea as a phylum. In elevating the Podocopa to a class, the author has followed the concept of Müller in the Bay of Naples monograph (Müller, 1894) rather than that of Sars, since for Müller Podocopa include podocopes and platycopes and this is also the author's assessment (McKenzie, 1972a). Heirarchic elevation of the Ostracoda and Podocopa cuts out the need to create new categories, such as cohort, in order to accommodate crustacean diversity at high heirarchic levels (Dahl, 1963). Podocopida remain a group of ordinal status although Sylvester-Bradley's concept has been restricted, and, similarly, Podocopina and Cytheracea retain their levels according to the American Treatise.

The significance of the new family stems from the fact that, while of predominantly cytheracean affinities, it does possess some significant features which characterize the superfamily Cypridacea. A statement such as the above must be justified in terms of taxa which could be considered to constitute typical cytheraceans and cypridaceans. Employing the chronological principle, since Bythocytheridae are are the longest surviving cytheraceans, comparisons will be made between *Bonaducecythere* and such genera as *Jonesia* Brady, 1866 and *Bythocythere* Sars, 1866. Further, since several cypridacean genera have a long fossil record in marine sediments, the cypridacean comparisons will be made with such genera as *Pontocypris* Sars, 1866 and *Macrocypris* Brady, 1868 because males are known in both rather than with the about equally long-lived genus *Paracypris* Sars, 1866 for which a male has yet to be described.

Like other cytheraceans, Bonaducecythere has a flagelliform exopod on the antenna, unlike the small plate bearing 3 unequally long setae which occurs on Macrocupris and most cypridaceans. Further, the antennal endopod is not adapted for swimming by carrying long natatory setae as it is in Pontocypris and many other cypridaceans. Bonaducecythere has 3 pediform thoracic limbs (PI to PIII). This feature is characteristic of all cytheraceans, as opposed to the reduced PI, pediform PII and reflexed PIII which typify all cypridaceans, including Pontocypris and Macrocypris. Thirdly, Bonaducecythere either has no furca or else has a very minute furca which could not be observed following dissection. All cytheraceans, including Jonesia and Bythocythere, are similar in this respect but a prominent and powerful furca is typical of many cypridaceans, including Pontocypris. Whereas in cypridaceans the PI has an exopod which is usually modified as a food forwarding structure and an epipod is often present, in Bonaducecythere exopod and epipod are absent and the PI is wholly pediform in the female but dimorphic and probably a clasping structure, fuctional during reproductive activity, in the male. Dimorphic thoracic limbs are not unknown in cytheraceans; witness the male PIII in Jonesia. The apparent absence of Zenkers Organs or such specialized ejaculatory apparati as occur in Pontocypris and Macrocypris is an anomalous feature. Finally, the muscle scars and radial pore canal pattern are wholly cytheracean.

On the other hand, *Bonaducecythere* in common with most cypridaceans has 4-segmented thoracic limb endopods (except in the male PI), a clasping type unguis on the male PI and large loops of seminal vesicles coiled within the duplicature.

McKenzie and Kaesler (1975) have indicated that reduction in the

numbers of segments in individual ostracodan limbs is likely an evolutionary trend within the subphylum. On this assumption, *Bonaducecythere* is more primitive than most other cytheraceans since it has 4—rather than 3—segmented thoracic limb endopods. Another podocopine genus, *Terrestricythere* Schornikov, 1969, which belongs in the superfamily *Terrestricytheracea* (Schornikov, 1969, n. comb. Hartmann and Puri, 1974) has a 4-segmented endopod on the walking leg (PII) and a clasping unguis on the male PI. Like *Bonaducecythere*, *Terrestricythere* is known only from modern environments. Such taxa, embodying features which may be regarded as primitive, offer a challenge to palaeontologists to find fossil representatives since they can scarcely have evolved at these high heirarchic levels within the Recent.

It has been pointed out that 4-segmented PII endopods also occur in cypridaceans and it can be added that they are typical, too, of living healdiaceans and darwinulaceans. The author, on a variety of grounds, places these 3 superfamilies in the suborder Metacopina (Palaeozoic to Recent) an interpretation of relationships which have been recently criticized and defended (Schornikov and Gramm, 1974, Maddocks, 1973, Mc-Kenzie, in press).

Then, there is the problem provided by the loops of seminal vesicles in *Bonaducecythere* males. Similar structures only occur in cypridaceans and the impressions of these loops on the inner valve surface are the main means by which sex dimorphism can be confirmed in fossil populations from Cenozoic assemblages. This striking similarity in part of the reproductive systems of taxa referred respectively to Podocopina and Metacopina, throws into focus Dainelopol's opinion that all podocopids should be considered as belonging in a single group rather than into the 2 or more subgroups into which they have been divided by other authorities (Danielopol, 1972).

Summarizing, the description of *Bonaducecythere hartmanni* indicates no features which are unique among the Podocopida; one feature, the expanded seminal vesicles, which is unique among Podocopina (as the suborder is understood by this author); and a few features which are unique for families in the Cytheracea. The totality of evidence tends to maintain the scheme proposed by the author in 1972, except that the subphylum rank of Ostracoda is now specified and Podocopa and Myodocopa are elevated to class rank. It remains the author's opinion, therefore, that Ostracoda (Cambrian-Recent) in terms of living taxa may be divided into Podocopa (Ordovician-Recent) and Myodocopa (Ordovician-Recent). The class Podocopa consists of the orders Podocopida (Ordovician-Recent) and Platycopida (Ordovician-Recent). Podocopida comprise the suborders Podocopina (Ordovician-Recent) with the superfamilies Bairdiacea (Ordovician-Recent); Cytheracea (Devonian-Recent) and Terrestricytheracea (?-Recent); and Metacopina (Ordovician-Recent) comprising the superfamilies Darwinulacea (Carboniferous-Recent); Cypridacea (Devonian-Recent); Healdiacea (Ordovician-Recent). It is necessary to add that this view does not represent a consensus: in particular, Gramm and his co-workers have criticized the placement of the living taxon *Saipanetta* in Healdiacea (e.g. Schornikov and Gramm, 1974). Nevertheless, the author's view is consistent with the results of a numerical cladistics study recently reported by Maddocks in which the taxa here regarded as podocopine cluster on one branch of a Wagner tree whereas those regarded as metacopine cluster on another (Maddocks, in press).

Types.—Stored at the British Museum (Natural History). Holotype δ : BM(NH) 1976.1369. Paratypes: \mathcal{P} , BM(NH) 1976.1370; 1δ , $4\mathcal{P}$, BM(NH) 1976.1371–1375. A second collection made at the type-locality is retained at Stazione Zoologica, Naples.

Acknowledgments

The material was collected by Dr. G. Bonaduce, of Stazione Zoologica, Napoli, Italia. The female dissection was made by Prof. Dr. G. Hartmann, University of Hamburg and the dissection of the male was completed by the author using the facilities of the British Museum (Natural History). Miss A. Scutt typed the manuscript.

Literature Cited

- Anderson, D. T. 1973. Embryology and phylogeny of annelids and arthropods. Pergammon, London, 475 pp.
- Dahl, E. 1963. Main evolutionary lines among recent crustacea. Pp. 1–26 in H. B. Whittington and W. D. I. Rolfe eds. Phylogeny and Evolution of Crustacea. Spec. Publ. Mus. Comp. Zool. Harvard, xi + 192 pp.
- Danielopol, D. L. 1972. Supplementary data on the morphology of Neonesidea and remarks on the systematic position of the family Bairdidae (Ostracoda: Podocopida). Proc. Biol. Soc. Wash. 85:39-48.
- Grundel, J. 1967. Zur Grossgliederung der Ordnung Podocopida G. W. Muller, 1894 (Ostracoda). Neues Jb. Geol. Palaont. Mh., 6:321–332.
- Hartmann, G. 1973. Zum gegenwartigen Stand der erforschung der Ostracoden interstitieller systeme. Ann. Speleol. 28:417–426.
 - ------, and Puri, H. S. 1974. Summary of neontological and paleontological classification of Ostracoda. Mitt Hamburgischen Zool. Mus. Inst. 70:7–73.
- Kornicker, L. S. 1974. Revision of the Cypridinacea of the Gulf of Naples (Ostracoda). Smithsonian Contr. Zool. 178:64 pp.
 - —, and I. G. Sohn. 1976. Evolution of the Entomoconchacea. Pages 55–61 in G. Hartmann, ed. Proceedings of the Fifth International Symposium on Evolution of Post-Paleozoic Ostracoda. Abh. Verh. Naturwiss. Ver. Hamburg, (NF) 18/19 (Suppl.):336 pp.
- Kozur, H. 1972. Einige Bemerkungen zur Systematik der Ostracoden und Beschreibung neuer Platycopida aus der Trias Ungarns. Mitt. Geol. Palaont., Innsbruck, 2:1–27.

272

- Maddocks, R. F. 1973. Zenker's organ and a new species of Saipanetta (Ostracoda). Micropaleontology 19:193-208.
 - ——. in press. Quest for the ancestral podocopid; numerical cladistic analysis of ostracode appendages, a preliminary report. In G. Hartmann, ed. Evolution of Post-Paleozoic Ostracoda.
- Manton, S. M. 1973. Arthropod phylogeny—a modern synthesis. J. Zool., Lond. 171:111–130.

McKenzie, K. G. 1970. Review. Crustaceana 19:110-112.

- ——. 1972a. Contribution to the ontogeny and phylogeny of Ostracoda. Proc. IPU, XXIII int. geol. Cong., Prague, 165–188.
 - —. 1972b. New data on the ostracode genera Laocoonella de Vos and Stock, *Redekea* de Vos, and *Aspidoconcha* de Vos; with a key to the family Xestoleberididae and a resume of symbiosis in Ostracoda. Beaufortia, 19:151–162.
 - —. 1975. Saipanetta and the classification of podocopid Ostracoda: a reply to Schornikov and Gramm (1974). Crustaceana 29:222–224.
- ——, and Kaesler, R. L. 1975. An introduction to the numerical phylogeny and classification of paradoxostomatid Ostracoda, including a re-description of *Machaerina tenuissima* (Norman), 1869. *In* F. M. Swain, ed., The biology and paleobiology of Ostracoda.
- Moore, R. C. (Ed.) 1961. Treatise on Invertebrate Paleontology. Pt. Q. Arthropoda.
 3. Crustacea: Ostracoda, Geol. Soc. America, Lawrence, Kansas, xxiii + 422 pp.
- Müller, G. W. 1894. Ostracoden. Fauna Flora Golfes Neapel, Monogr. 21:i–viii, 1–404.
- Orlov, Yu. A. (Ed.) 1960. Basic Paleontology. Trilobitamorpha and Crustaceamorpha. Acad. Sci. USSR. Moscow, 515 pp. (Russian).
- Poulsen, E. M. 1969. Ostracoda-Myodocopa Part III A Halocypriformes—Thaumatocypridae and Halocypridae. Dana Rep. 75:100 pp.
- Runnegar, B. and J. Pojeta, Jr. 1974. Molluscan phylogeny: the paleontological viewpoint. Science 186:311–317.
- Schornikov, E. I. 1969. A new family of Ostracoda from the supralittoral zone of the Kurile Islands. Zool. Zhurnal 68:494–498 (Russian).
 - —, and M. N. Gramm. 1974. Saipanetta McKenzie, 1968 (Ostracoda) from the northern Pacific and some problems of classification. Crustaceana 27: 92–102.

Riverina College of Advanced Education, P.O. Box 588, Wagga Wagga, N.S.W. 2650, Australia.